

THE PHYTOGEOGRAPHIC SIGNIFICANCE OF SOME EXTINCT GONDWANA POLLEN TYPES FROM THE TERTIARY OF THE SOUTHWESTERN CAPE (SOUTH AFRICA)¹

J. A. COETZEE² AND J. MULLER†

ABSTRACT

Pollen assemblages of lower Miocene age from sediments in the southwestern Cape contain ancient Gondwana microfloras of considerable phytogeographic interest. The parent taxa, which are not represented in Africa today, indicate the existence of subtropical rain forest in these regions during the Tertiary. This microfossil record supports the hypothesis that a common South American–Antarctic–African–Madagascar flora existed in the Gondwana fragments during the Cretaceous. The final extermination of these elements in the southwestern Cape at the close of the Tertiary was probably related to the wide ranging effects of the glaciation of Antarctica. Sclerophyllous macchia has since become dominant and adapted to the present Mediterranean climate.

The unique flora of the southwestern Cape is very well known for its species richness and high degree of endemism. This vegetation, which belongs to the phytochorion *Capensis* (Taylor, 1978; Werger, 1978), occurs in the present summer-dry/winter-wet climate of the region. It does, however, extend eastward to the vicinity of Port Elizabeth, which receives precipitation all year. Interesting outliers of this sclerophyllous vegetation also occur at increasing altitudes to the north in the mountains of the Karoo and Namaqualand and along the eastern mountain chain as far as Ethiopia (Axelrod & Raven, 1978; Taylor, 1978). With regard to its history and phytogeography, the dominant sclerophyllous macchia (*fynbos*) of *Capensis* has been the focus of interest for a long time. Only in recent years have palynological investigations shown that this vegetation type, adapted to a Mediterranean climate, is not as old as previously thought (Coetzee, 1978, 1983). Pollen assemblages of Tertiary age from boreholes at Noordhoek on the Cape Peninsula and in the Saldanha region, both on the Atlantic margin, now indicate that entirely different vegetation and climates compared with the present had existed in the southwestern Cape.

Some of the fossil pollen types belong to ancient parent taxa that are extinct in Africa today

(Coetzee, 1981; Coetzee & Praglowski, 1984). In this connection the pollen assemblages from Noordhoek on the Cape Peninsula are of particular interest and will be mainly referred to in this discussion (Figs. 1–7). Further investigation of the pollen spectra has provided additional evidence of other extinct types and, because these records are of considerable phytogeographic interest, they will be discussed in relation to their past distribution and paleoecology.

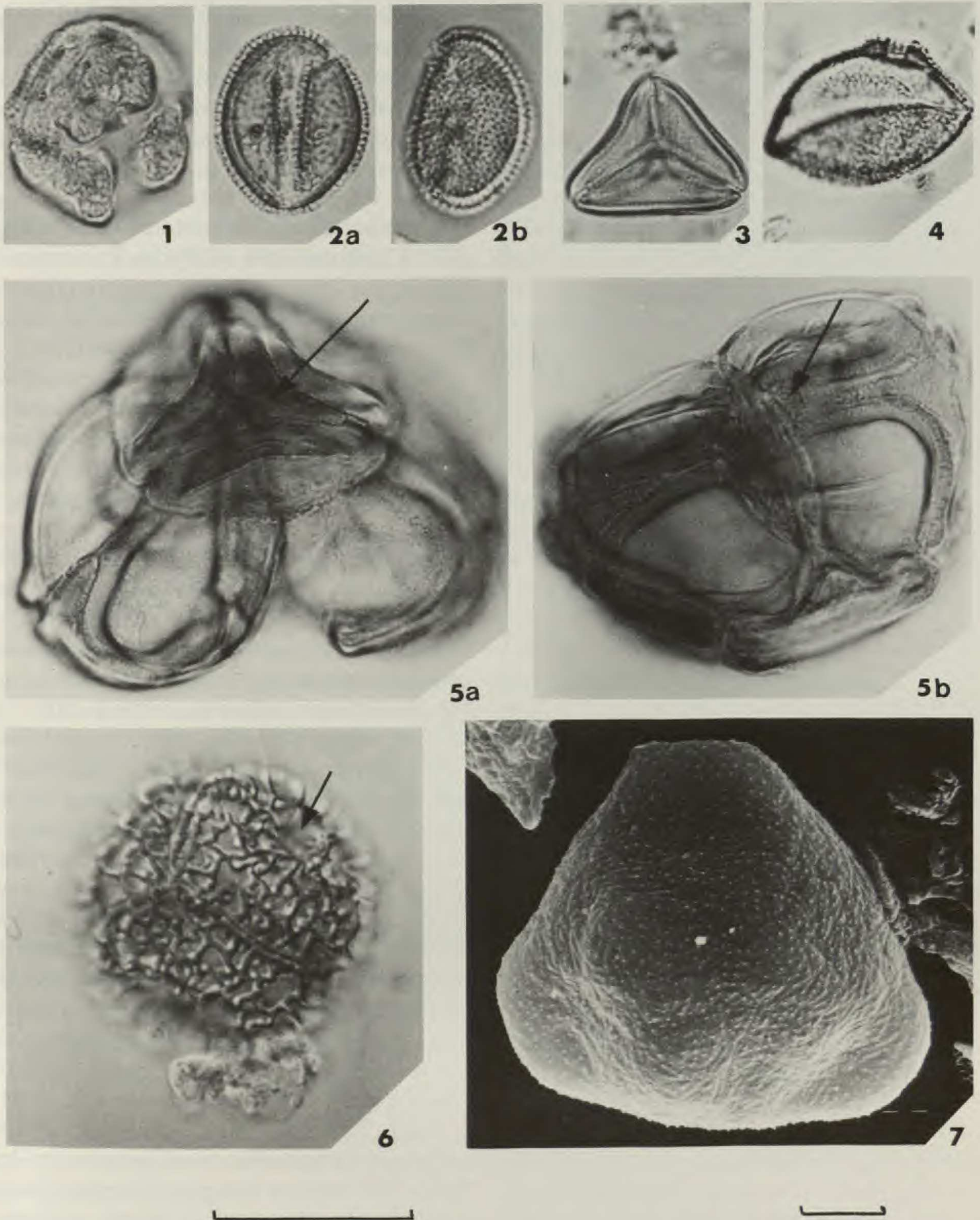
Two pollen assemblages have been distinguished. The older assemblage contains seven extinct pollen types, some of which are significant for the explanation of present disjunct distribution patterns of genera in the Southern Hemisphere. The younger assemblage does not contain these extinct microfossils but is characterized by the pollen of macchia (*fynbos*) vegetation of a type dominant in the region today.

LITHOLOGY AND AGE OF THE NOORDHOEK SEDIMENTS

A pocket of sediments containing pollen-bearing peaty clay horizons occurs within 2 km of the present coastline in a fault-controlled valley flanked by mountains, between Noordhoek and Kommetjie (34°09'S and 18°20'E) on the Cape

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² Institute for Environmental Sciences, University of the Orange Free State, Bloemfontein, South Africa.



FIGURES 1-7. Extinct pollen types.—1. *Microcachrys* (Coniferae), Noordhoek 5836 no. 27, high focus. 2. *Ascarina*-type (Chloranthaceae).—2a. (cf. *A. rubricaulis*-type), Noordhoek 5836 no. 25, holotype, optical section.—2b. (cf. *A. phillipensis*-type), Noordhoek 5836 no. 36, holotype, Nomarski interference contrast, lateral view.—3. *Cupaniopsis*-type (Cupanieae, Sapindaceae), Saldanha, S1 7115 (co-ord. 7.6, 68.4).—4. *Sparganiaceapollenites barungensis* Harris, Noordhoek 5836 (co-ord. 16.2, 72.6), median focus showing annulate pore. 5. *Xyloolaena*-type (Sarcolaenaceae), Noordhoek 7269.—5a. no. 9, holotype, tetrad at high focus level showing triangular island (arrow) enclosed by 3 ridges.—5b. no. 10, paratype, view of tetrad with common aperture (arrow) between 2 grains.—6. Winteraceae (*Bubbia*-type), Noordhoek 5836, no. 8, tetrad at high focus showing pore (arrow), Nomarski interference contrast.—7. Casuarinaceae, Noordhoek 7241, SEM micrograph showing spinules on linear ridges. Scale bar = 25 μm (nos. 1-6) and 10 μm (no. 7).

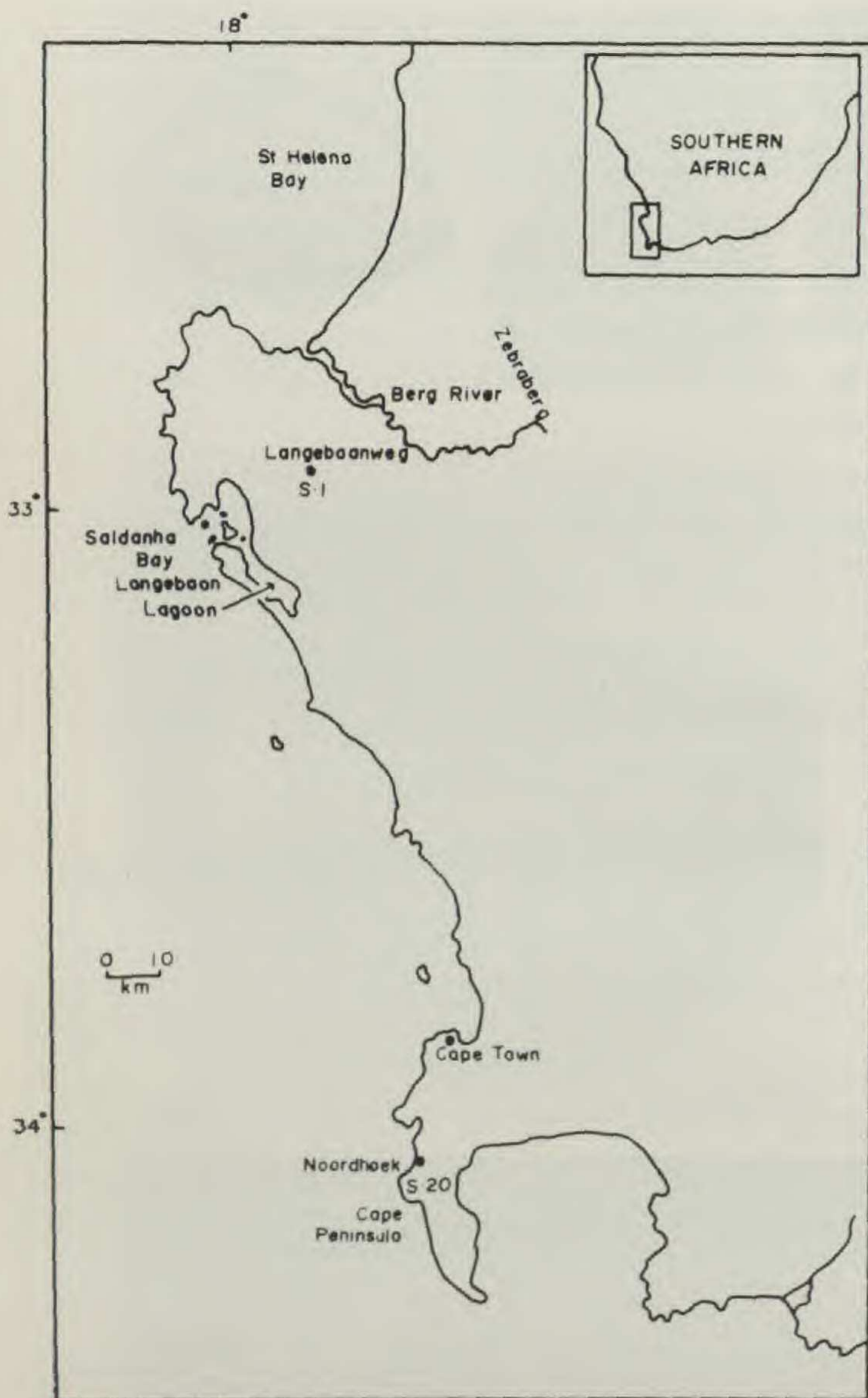


FIGURE 8. Locality map.

Peninsula (Fig. 8). These sediments, which lie below sea-level, have been subdivided into the following two Formations according to the sedimentological profile (Rogers, 1980): Bredasdorp Formation (Noordhoek member, -21 to 0 m) and Elandsfontyn Formation (-21 to -50 m). The Elandsfontyn Formation, characterized by coarse angular quartz sand, contains the bulk of the organic matter in the succession and shows no marine components. It is in this Formation that the older Tertiary pollen assemblage mainly occurs, while the younger assemblage falls mainly within the Noordhoek member of the Bredasdorp Formation. Here at -10 m rare sponge spicules are the only marine components. Further detailed parallel palynological and lithological investigations on these sediments are to be carried out in connection with paleoenvironmental assessments.

In the absence of present possibilities for firm age control the palynological assemblages of the

Elandsfontyn Formation at Noordhoek previously had been assigned a relative Late Oligocene/Early Miocene age (Coetzee, 1978, 1983). This derivation had been made by comparison of the pollen types with apparently younger palynological assemblages in the Elandsfontyn Formation belonging to sediments further north in the Saldanha region. Here in Borehole S1 (33°58.20'S and 18°6.97'E) this Formation fits as follows into the succession that contains the paleontologically dated Early Pliocene Varswater Formation (Coetzee & Rogers, 1982):

Varswater Formation, Early Pliocene (vertebrate fauna) (Hendey, 1981a, 1981b).

"Saldanha" Formation (gravel member), Late Miocene (Tankard, 1975; Hendey, 1981a, 1981b) (now considered to be younger).

Elandsfontyn Formation, Early to Middle Miocene (Coetzee, 1980) (now considered to be younger).

Further palynological considerations by the present authors now confirm a Miocene age for the Noordhoek pollen assemblages and suggest an early rather than late Miocene age. Comparison is hardly possible with the well dated tropical Tertiary microfloral succession of Gabon (Salard-Cheboldaeff, 1979), Nigeria (Germeraad et al., 1968), and Senegal (Médus, 1975) because of the subtropical aspect of the Noordhoek microfloras. Only a few fossil pollen types are common to all these regions. A more direct comparison is, however, possible with the ecologically similar assemblages from the Ninetyeast Ridge and Australia. The time of the extinction of taxa obviously can not be used for age-comparisons. However, the first occurrence of widespread types is more significant and in this connection the pollen of Compositae is of paramount importance. The earliest records of the Tubiflora type are from the Oligocene of North America, Europe, and Ninetyeast Ridge, where they always occur in very low frequencies. They become more common worldwide in the Miocene (Muller, 1981). The fairly regular but sparse occurrence of Compositae pollen grains of the Tubiflora type with very low diversity in the older assemblage of Noordhoek suggests a Lower Miocene age for these pollen-bearing horizons. Unfortunately a section between the older and younger assemblages contains no pollen and probably indicates a hiatus in deposition that is difficult to explain until the detailed correlation of the lithology and palynology has been completed. This may be

confirmed by the initial sharp increase and high diversity of Compositae in the younger assemblage. Such high numbers of Compositae pollen are characteristic of Upper Miocene and Pliocene or even Quaternary sediments.

GENERAL COMPOSITION AND FORMER DISTRIBUTION OF THE MICROFLORA

THE OLDER ASSEMBLAGE

Pollen of Podocarpaceae, *Widdringtonia*, Combretaceae (or *Dissotis* (Melastomataceae)), and Restionaceae are abundant at various periods whereas mostly low numbers of *Calodendrum* and Myrtaceae occur throughout the sequence. Pollen of Compositae and Gramineae are also very sparsely represented. These microfossils indicate the presence of elements of a temperate evergreen forest reminiscent of the present Afromontane forest enclaves in the Cape Province extending from east of Knysna, the Knysna forests, and the relict forest patches in valleys or "kloofs" of the Capensis phytochorion (Axelrod & Raven, 1978; Taylor, 1978; White, 1978). In addition abundant pollen was recorded of Palmae that are extinct in these regions today. These pollen types are different from those of the present South African palms, the southernmost of which, viz. *Phoenix* occurs near Bathurst in the eastern Cape. These microfossils together with pollen types such as *Croton*, Cupanieae, and others indicate the presence of subtropical floral elements. It is in this mixed type of vegetation that pollen of the following seven extinct taxa, already alluded to, has been recorded: *Microcachrys*, Winteraceae, Casuarinaceae, *Ascarina*-type, Sarcocaulaceae, *Cupaniopsis*-type, and *Sparganiaceapollenites barungensis*. Further discussions will center around these taxa.

THE YOUNGER ASSEMBLAGE

The dominant microfossils in this assemblage belong to the Proteaceae, Ericaceae, *Cliffortia*, Compositae, Chenopodiaceae, Gramineae, Cyperaceae, and Restionaceae with some Thymelaeaceae and occasional *Casuarina/Myrica* types. The contrast with the preceding assemblage is thus considerable.

THE EXTINCT POLLEN TYPES (FIGS. 1-7)

Microcachrys (Coniferae). The relatively rare but highly characteristic trisaccate *Microcachrys*

pollen (Fig. 1) is often associated in its occurrences with maxima of *Casuarina* pollen. At present the genus is restricted to Tasmania, where it occurs in the montane vegetation above 1,000 m. Its past distribution was much more extensive, and it has been reported from the Jurassic and Cretaceous of India, the Lower Cretaceous of Madagascar, the Jurassic, Cretaceous and Tertiary of Australia, the Lower Cretaceous-Tertiary of New Zealand, the Lower Cretaceous of Argentina, the Tertiary of Kerguelen, and the Paleocene and Oligocene of Ninetyeast Ridge (Archangelsky & Gamarro, 1967; Couper, 1960; Hengreen et al., 1982; Kemp & Harris, 1977; Venkatachala et al., 1972). Scott (1976) reported this pollen from the Lower Cretaceous of the Algoa Basin on the southeastern coast of South Africa, and more recently McLachlan and Pieterse (1978) recorded it from Lower and Upper Cretaceous sediments of the DSDP drilling site 361, 180 miles southwest of Cape Town.

Winteraceae. Tetrads of this family are also highly characteristic of the older pollen assemblage but occur scattered throughout the whole section. Two slightly different types appear to have been present. Comparison with the pollen morphological monograph of the family by Pragłowski (1979) and a joint study with him of his reference material indicate that the larger type has most likely been derived from *Drimys* section *Tasmannia*. This plant group is at present confined to Malesia, Australia, and Tasmania, where it occurs in tropical forest, subtropical to temperate rain forest, and subalpine shrub vegetation (Fig. 9). Its closest affinity lies with the pollen of *Drimys piperita*. The smaller type (Fig. 6), however, closely resembles the pollen of *Bubbia isoneura*, a New Caledonian species. The genus *Bubbia* occurs at present from sea-level to montane habitats in New Caledonia, New Guinea, and the Moluccas but is found in Australia only in Queensland and thus appears less well adapted to colder climates (W. Vink, oral comm.). The oldest record of Winteraceae is from the Aptian/Albian of Israel (Walker et al., 1983) and it is of special interest that this is the only other extant angiosperm family besides the Chloranthaceae which, so far known, has a Lower Cretaceous occurrence.

It is of interest to note that the South African fossil pollen types appear to be more related to Old World representatives of the family than to the New World group of *Drimys* section *Drimys*. They also differ from *Takhtajania perrieri* (*Bub-*

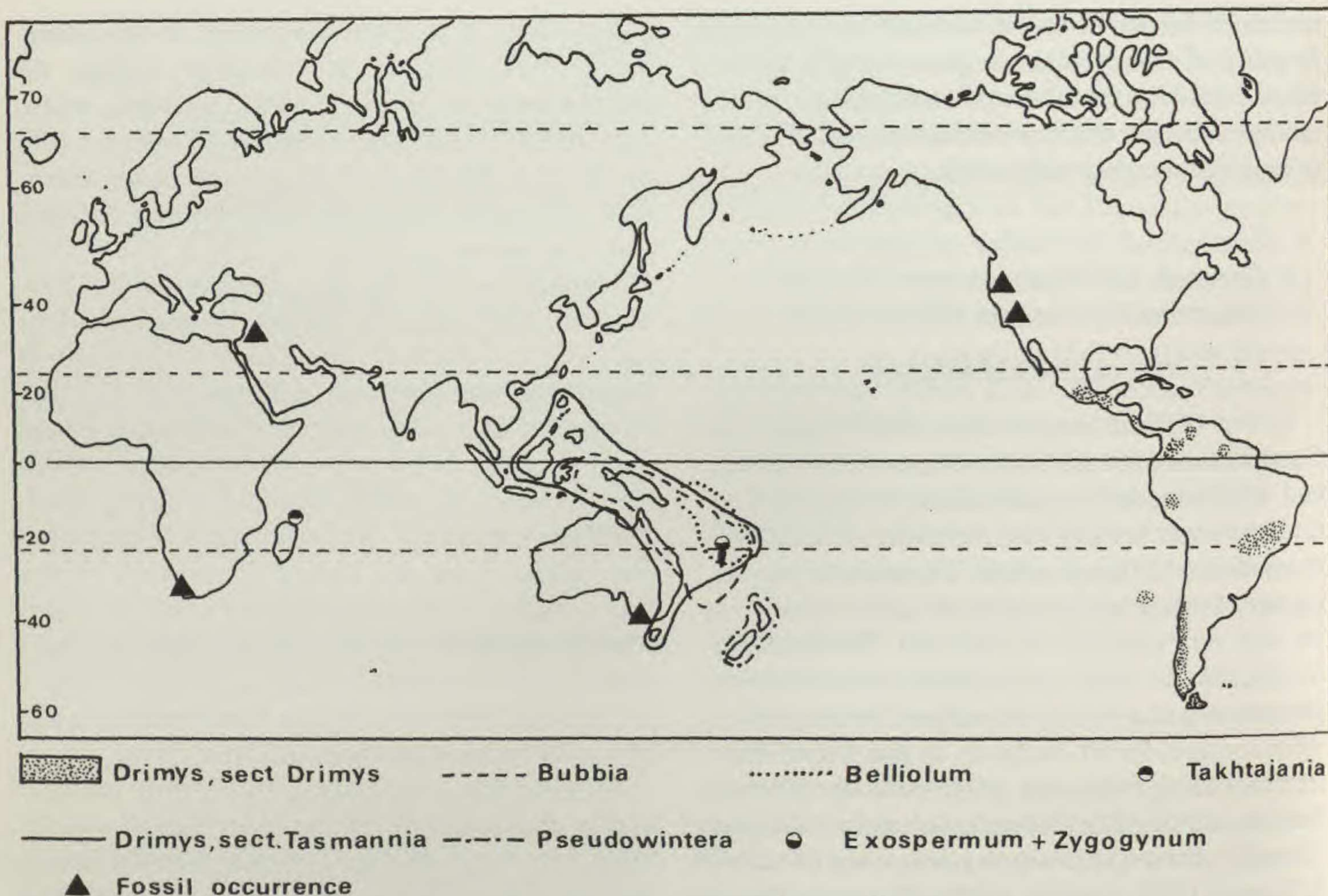


FIGURE 9. Distribution map of recent and fossil Winteraceae.

bia perrieri), the only representative of the family in Madagascar.

Fossil pollen of Winteraceae has been described from the Maestrichtian of South Australia and New Zealand as *Gephyrapollenites* by Stover and Partridge (1973), who recognized three species without indicating affinities with recent pollen types of the family. Martin (1978), however, pointed out that its closest relationship is with *Drimys* section *Tasmannia*. Mildenhall and Crosbie (1979) considered *Gephyrapollenites* a junior synonym of *Pseudowinterapollis*. They are of the opinion that this genus is similar to the recent endemic genus *Pseudowintera* of New Zealand. The specimens from South Africa do not fall within the circumspection of *Pseudowinterapollis* as previously thought by Coetzee (1981).

Casuarinaceae. The pollen type of this family (Fig. 7) is very common throughout the older assemblage and shows marked changes in abundance. The possibility that many of these forms could belong to this family has already been alluded to (Coetzee, 1983) and it has now been proved beyond doubt at the SEM and TEM levels by Praglowski (Coetzee & Praglowski, 1984) that Casuarinaceae existed in South Africa in the Ter-

tiary. The pollen can easily be confused at the light microscope level with that of *Myrica*, which also occurs in the assemblage (cf. also Muller, 1981).

Unfortunately it is not possible to differentiate between the pollen of the inland representatives of the family and that of the widespread *Casuarina equisetifolia*, which is a pioneer of tropical sandy beaches.

Casuarinaceae are adapted to a subtropical-tropical climate and are found today in a wide range of rainfall conditions. The main development of the family is undoubtedly centered in Australia with radiation into the Pacific and Southeast Asia, the range of *C. equisetifolia* being much wider. The probable native range of the family is indicated in Figure 10.

Fossil pollen has been found in abundance in Tertiary sediments of New Zealand, Australia, the Ninetyeast Ridge, and Borneo, and recorded as *Haloragacidites* (= *Triorites*) *harrisii* or as *Casuarinidites cainozoicus*. Macrofossils have been found in the Paleocene of Argentina, and the occurrences at Noordhoek fit in well with a formerly much wider range of the family.

Ascarina-type (*Chloranthaceae*). This pollen type (Fig. 2) is especially frequent in the lower

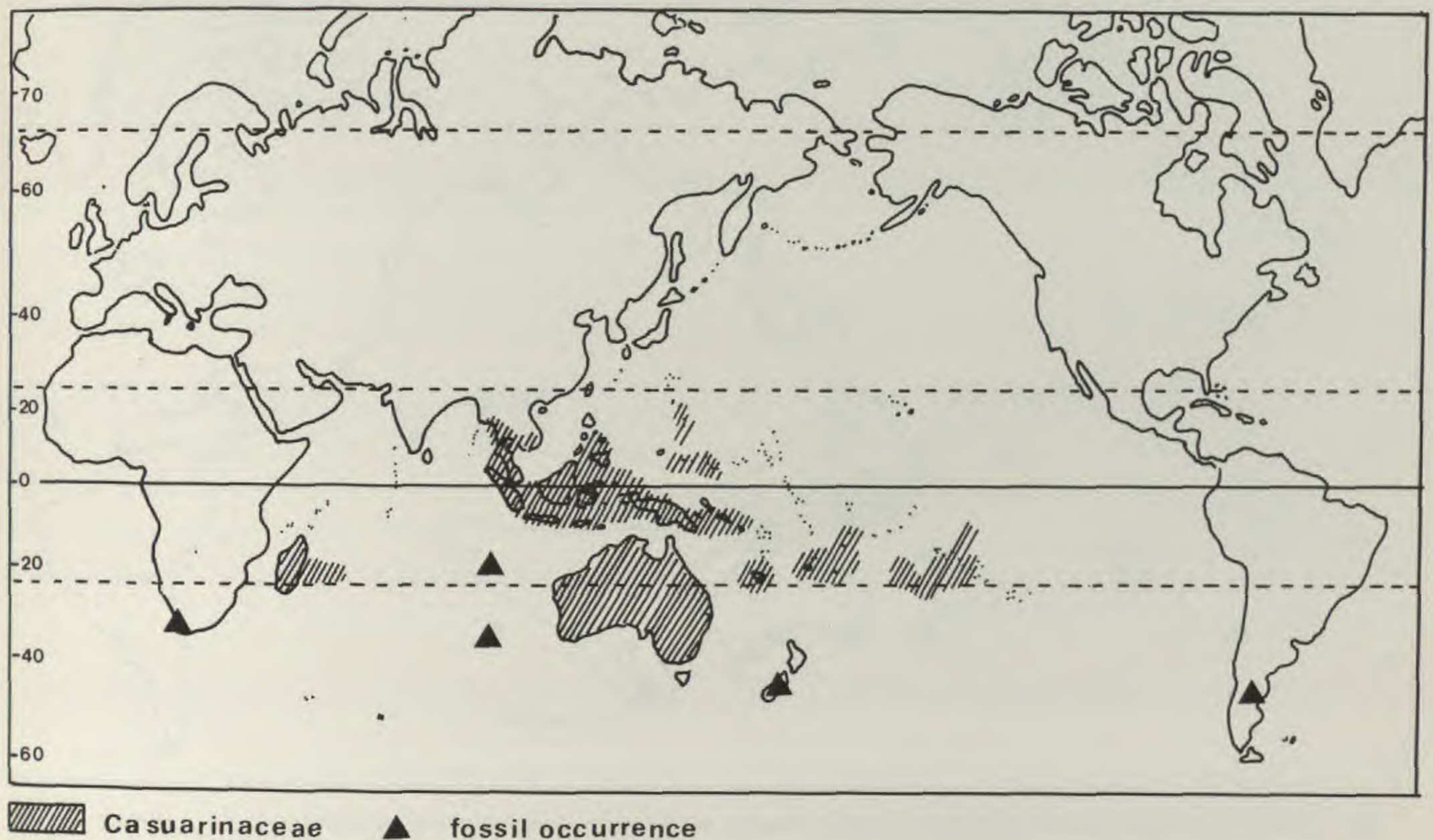


FIGURE 10. Distribution map of recent and fossil Casuarinaceae.

part of the section, where it alternates with maxima of *Casuarina*, *Microcachrys*, *Podocarpus*, *Widdringtonia*, Combretaceae/Melastomataceae, and Proteaceae pollen. More than one subtype comparable to *Ascarina rubricaulis* (Fig. 2a), *A. philippinensis* (Fig. 2b), and *Ascarinopsis coursii* appears to be present. The last species, often included in *Ascarina*, is a rare endemic found in humid montane forests at an altitude of 1,700–1,800 m in the northeast of Madagascar. The seven species of *Ascarina* occur in East Malesia and New Guinea in montane rain forest from 1,010–3,300 m and in the west Pacific in New Zealand also in a humid climate, but from sea-level to 1,500 m (Fig. 11).

In this case also, the fossil occurrence of *Ascarina* in the Miocene of South Africa fits in well with its formerly much more widespread range, which in the Palaeogene covered Australia and the Ninetyeast Ridge (Fig. 11). In the Cretaceous this pollen type (as *Clavatipollenites*) was even much more widespread, being found in central Africa, North and South America, and Europe (Muller, 1981) while it has been reported for the Lower Cretaceous by Scott (1976) from boreholes along the southeastern African coast, and by McLachlan and Pieterse (1978) from the DSDP site 361, 180 miles SW of Cape Town in the Upper Cretaceous sediments.

Xyloolaena-type (*Sarcolaenaceae*). The very

characteristic pollen tetrads of this type (Fig. 5) are restricted to the genera *Leptolaena*, *Rhodolaena*, *Sarcolaena*, and *Xyloolaena* of the family Sarcolaenaceae, which is endemic to Madagascar. These tetrads occur scattered in the lower part of the older assemblage and appear to resemble most closely the tetrads of *Xyloolaena* (Carlquist, 1964; Straka, 1964).

Sarcolaenaceae are shrubs or small trees, rarely large trees, which occur mainly as rare elements in the humid forests of the eastern region of the island. Here they prefer the drier localities on sandy or rocky soil over a wide range of altitudes but are found also on coastal dunes (*Sarcolaena*) or, rarely, in the dry eastern region (*Leptolaena arenaria*) (Cavaco, 1952; Perrier de la Bâthie, 1920).

Cupaniopsis-type (*Sapindaceae*). This pollen type (Fig. 3), which is equivalent to the fossil genus *Cupanieidites*, is at present restricted to part of the tribe Cupanieae from America, Madagascar, and Australasia while it is conspicuously missing in genera occurring in Africa (Muller & Leenhouts, 1976; Muller, 1981). The pollen occurs in comparatively low frequencies in the older assemblage and is not correlated with maxima of other pollen taxa.

The fossil pollen genus *Cupanieidites* was abundant in the Upper Cretaceous both of central Africa, becoming extinct here in the early

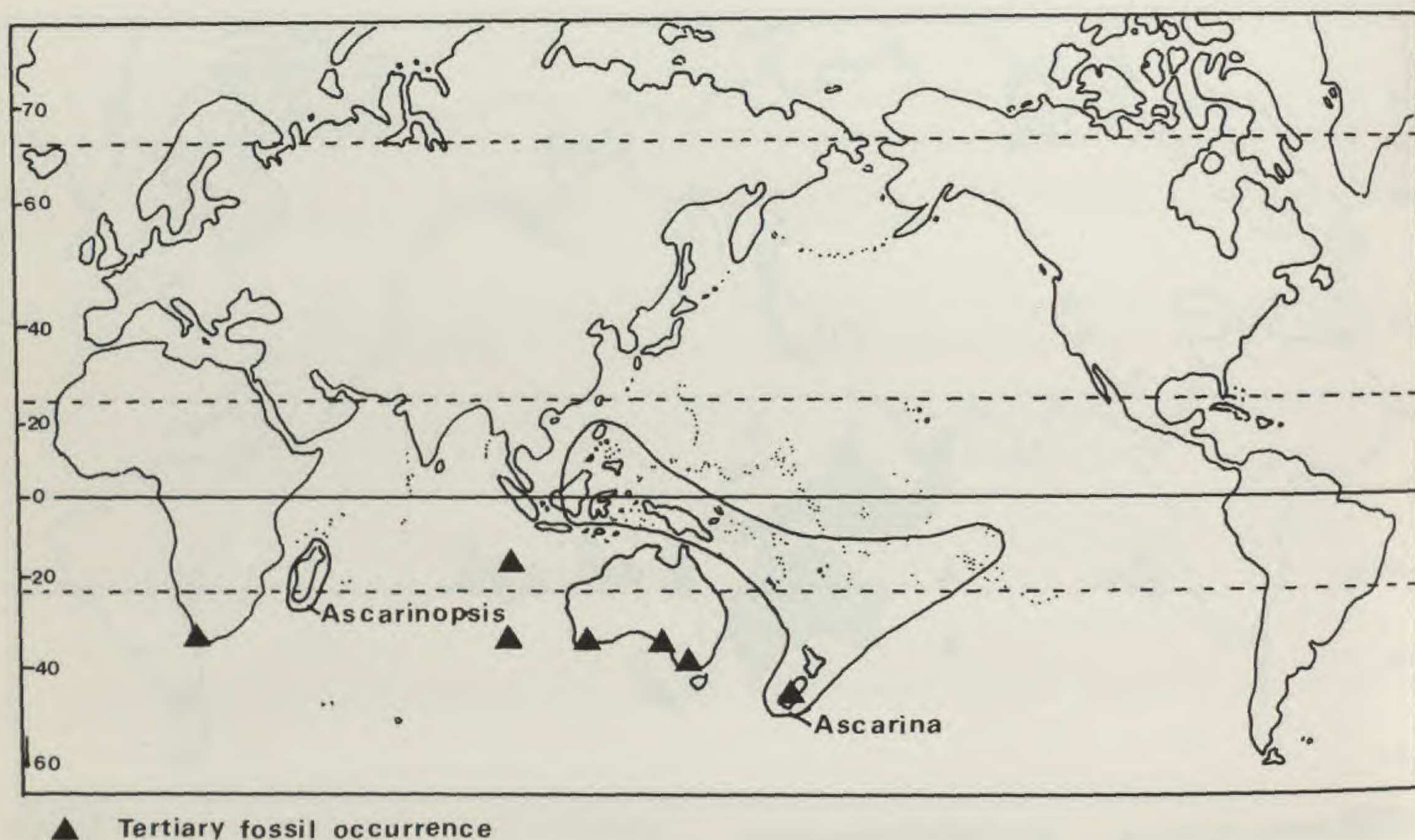


FIGURE 11. Distribution map of *Ascarina* and *Ascarinopsis* (Chloranthaceae) and Tertiary occurrences of fossil *Ascarina*-type pollen.

Tertiary (Muller & Leenhouts, 1976), and of South Africa from where it was reported from the Upper Cretaceous sediments from DSDP site 361 (McLachlan & Pieterse, 1978). *Cupanieidites* has an Upper Cretaceous record in Brazil and the earliest record for Australia is from the Palaeocene (Muller, 1981). The genera of Cupanieae with this pollen type occur at present in a wide range of humid tropical to subtropical environments (Fig. 12).

Sparganiaceapollenites barungenis Harris (*Typhales*) (*Aglaoreidia qualumis* Partridge). This pollen type (Fig. 4) probably has been derived from a taxon related to Typhaceae or Sparganiaceae but cannot be identified with a living species, although Martin (1973) suggested that the pollen of the living *Sparganium anti-podum* is rather similar.

In the older assemblage it is common and fluctuates greatly in abundance as does the pollen of Restionaceae. Both pollen types probably are derived from marsh vegetation around fresh water inland lakes.

The fossil pollen type was first described from the Eocene–Miocene of Australia and New Zealand (Harris, 1972; Mildenhall & Crosbie, 1979). *Sparganiaceapollenites* has also been recorded from the Palaeocene of Argentina (Archangelsky, 1973).

DISCUSSION

In general the Miocene pollen flora of the southwestern Cape, the composition of which has been broadly discussed by Coetzee (1978, 1983), appears to represent lowland and montane subtropical rain forest in which palms were prominent. This vegetation type does not occur in the area at present although the Knysna forest to the southeast possibly could be considered an impoverished remnant of it. This flora clearly antedates the development of a Mediterranean climate in the Cape region, possibly in the Pliocene (Hendey, 1981b) or Late Pleistocene (Axelrod & Raven, 1978), as discussed by Coetzee (1983). The humid forest in Madagascar that at present contains taxa similar to those of the Miocene rain forest of the Cape (*Ascarinopsis*, Cupanieae, Winteraceae, and Sarcolaenaceae) is also a modified descendant from this ancient vegetation type, which was postulated by Axelrod and Raven (1978, Fig. 6) to have been present in the Late Miocene in both regions.

It is obvious from the pollen assemblages that links existed with the ancient floras of Gondwanaland (Raven & Axelrod, 1974). These floras may have dispersed almost directly among the closely situated Gondwana fragments, possibly from the mid-Cretaceous to the Palaeogene.

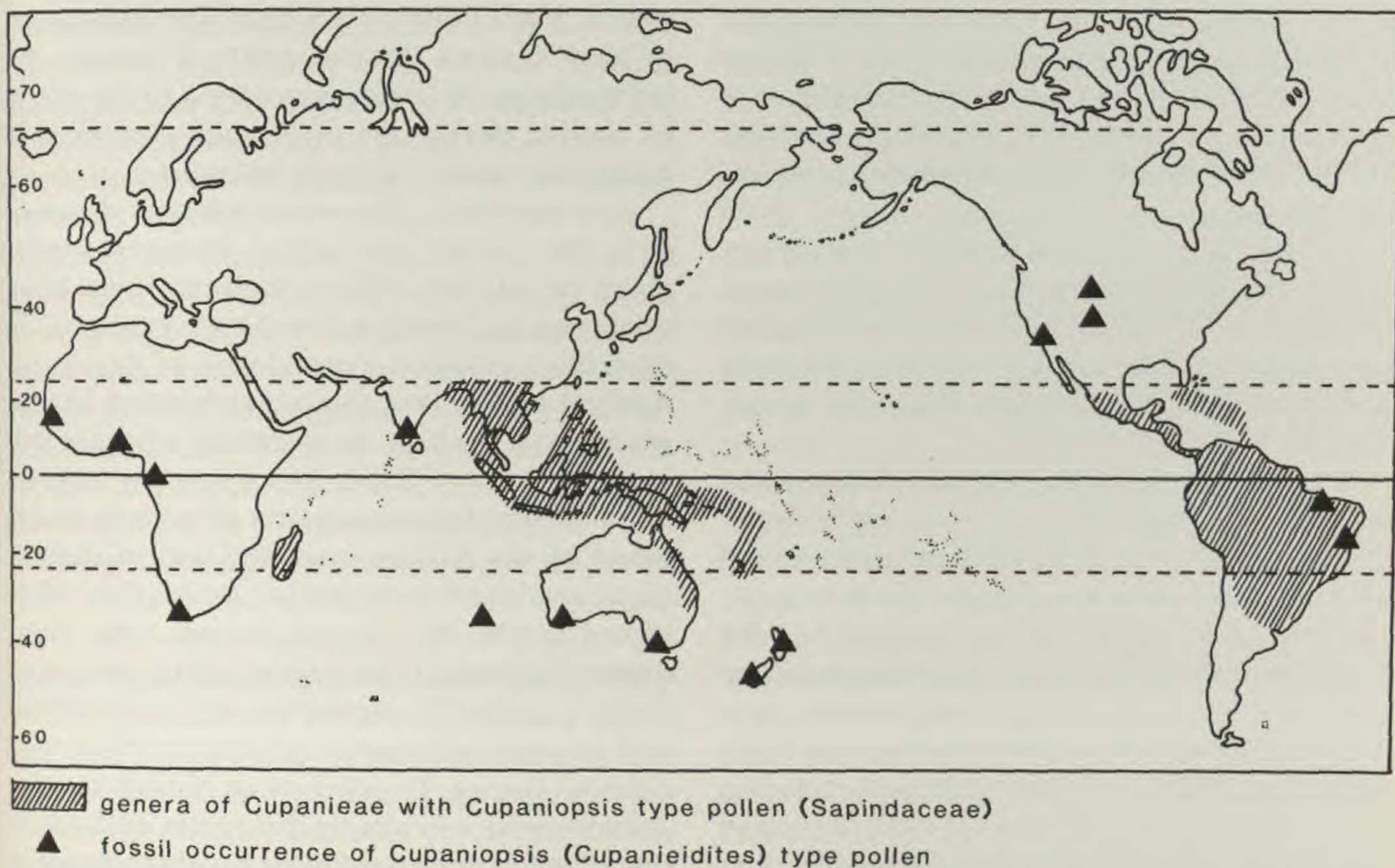


FIGURE 12. Distribution map of genera of Cupanieae with *Cupaniopsis*-type pollen and fossil occurrences.

In these latter periods the dispersal routes were either tropical or subtropical or more temperate with Antarctica in both cases in the central position (Raven & Axelrod, 1974).

With regard to the common Africa-Madagascar floral elements, recent geophysical evidence (Rabinowitz et al., 1983) indicates that the motion of Madagascar relative to Africa was from the north and probably started in the mid-Jurassic (165 million years ago) or somewhat later depending on the postulated spreading rates. Separation from the continental margin of Kenya and Somalia must have been effective at least from the Cenomanian (95 million years ago) onward. This is confirmed by the presence, in the Albian of Madagascar, of a microflora indicative of the Gondwana province of Herngreen and Chlonova (1981; Herngreen et al., 1982), suggesting southern contacts rather than east African ones at that time. Raven and Axelrod (1974) and Axelrod and Raven (1978) visualized these connections, via the now largely submerged Mascarene plateau, with India and Antarctica and lasting till the late Cretaceous. This connection then could have provided a route for the Cretaceous dinosaurs as well as for the rich angio-

sperm floras of Madagascar and the Seychelles.

Microcachrys. This is undoubtedly the most prominent ancient Gondwana element with a probable continuous range in the Cape region from the Lower Cretaceous into the Miocene. The records of the former distribution of *Microcachrys*, as discussed earlier, are all from ancient fragments of Gondwanaland. This former range is in sharp contrast with the present day relict occurrence in Tasmania. The genus may have originated in the Jurassic or earlier and dispersed widely in the Jurassic-Lower Cretaceous, after which it became variably extinct. It is of special interest that *Microcachrys* survived much longer in South Africa than in India, which, during its northward drift, passed through totally different climatic zones. It is interesting that another Mesozoic gymnosperm genus, *Araucaria* (*Araucariacites*), the pollen of which occurs concomitantly with *Microcachrys* in the Cretaceous of South Africa (McLachlan & Pieterse, 1978; Scott, 1976), did not survive as long as *Microcachrys* in the Cape.

Winteraceae. Like the other ancient angiosperms represented in the Tertiary pollen assemblages, this family forms a specific link with the

austral floras, especially with the subtropical-temperate types. Of importance is the evidence in the Miocene of the Cape of representatives of the Australasian group of Winteraceae. That this family was formerly more widespread was already suggested by the discovery of fossil wood in the Upper Cretaceous of North America (Page, 1981). The nature of the wood has suggested a relationship with the Old World Winteraceae but the anatomical features are now thought to be correlated with climate rather than with taxonomy (P. Baas, oral comm.).

The primitive characters of the Winteraceae are well in accord with at least an early Cretaceous origin as indicated by the presence of fossil pollen attributed to this family (Walker et al., 1983) in Israel, which formed part of the ASA floral province at that time. According to Hergreen and Chlonova (1981) this province covered the tropical-subtropical zone of a joint South American-African-Arabian continent including Israel, and overland dispersal in Gondwanaland was clearly possible in the early Cretaceous. The survival of the related genus *Takhtajania* in Madagascar indicates local evolution also from an ancient Gondwana matrix. To reach Madagascar the dispersal to this island must, according to Axelrod and Raven (1978), have occurred before 80 million years ago. In view of its early separation from Africa, dispersal was probably from the south. Raven and Axelrod (1974: 616) inferred that the ancestors of the Winteraceae reached Australia in mid-Cretaceous time along a tropical or subtropical route.

The present day American representatives of the Winteraceae grouped in *Drimys* section *Drimys* may be a later development from West Gondwana ancestors, separate from development in Australia.

The records for *Casuarina*, *Ascarina*, and *Cupanieae*, which will be discussed next, refer to elements that are less clearly restricted to temperate, subtropical, or montane tropical climates.

Casuarinaceae. This family is found in tropical lowland, montane, and subtropical climates. Fossil and present day distributions point to a wide range in the past covering the Pacific, Southeast Asia, Australia, Madagascar, and the southern parts of Africa and America (Fig. 10). Raven and Axelrod (1974: 616) suggested that the ancestors of Casuarinaceae may have reached Australia in mid-Cretaceous times by a subtropical to tropical route from Africa. The oldest-

known fossil pollen dates from the Palaeocene of New Zealand (Muller, 1981). Evidently the contraction of its range was related to the effects of cooling during the maximum glaciation of Antarctica in the Terminal Miocene.

Ascarina-type. The relationship of *Ascarina* with the Lower Cretaceous *Clavatipollenites* group (cf. Muller, 1981), which may even have originated in Central Africa (Doyle et al., 1977), most likely refutes the postulation of Raven and Axelrod (1974) that this genus reached Madagascar from the east. Its abundant presence still in the Miocene of South Africa strongly suggests that a chloranthaceous matrix developed somewhere on the African mainland and its descendants could easily have reached Madagascar while spreading out over Antarctica and other Gondwana fragments. The marked contraction of its range is probably connected with competition with younger angiosperm groups as well as with climatic change. Its survival in Madagascar (as *Ascarinopsis*) is evidently due to the isolation of this island and the continued equable climate at these latitudes. The climatic requirements may have been more subtropical to tropical-montane than was the case with *Casuarina*.

Cupanieae. Cupanieae have also had a long history on the African continent as is shown by the abundance of *Cupaniopsis*-type pollen in the Upper Cretaceous of West Central Africa and the Miocene of South Africa. They presumably reached Madagascar in mid-Cretaceous time after it separated from East Africa.

The range contraction of those genera of Cupanieae that were characterized by *Cupaniopsis*-type pollen was completed much earlier in tropical central Africa than in the subtropical southern region where some taxa still survived in the Miocene. The explanation for the extinction of part of the Cupanieae in Africa is at present obscure. In Madagascar the genera *Molinaea* and *Tina* of this group have survived until the present day and are widespread from sea-level up to more than 2,000 m. In Australasia and America the genera of this group are still widespread today and range from tropical to subtropical temperate climates (Fig. 12).

Xyloolaena-type. For Sarcocaulaceae a similar development may be postulated, although a comparable fossil record is lacking. The occurrence in South Africa of the highly developed *Xyloolaena*-type in the Miocene of the Southwestern Cape is the first fossil record of the family but certainly does not represent the oldest oc-

currence of the Sarcolaenaceae. It is not clear whether we are dealing here with an endemic African family that migrated to Madagascar and later become restricted to the island, as was inferred by Raven and Axelrod (1974). Its ecology, although slightly more specialized than that of *Ascarina* and Cupanieae, still fits into a humid subtropical to tropical-montane pattern. These three groups probably occurred together in the same forest type that they inhabit today in the humid forest of Madagascar. The history of Sarcolaenaceae and *Ascarina* appears to be comparable and the contraction of their ranges may have been due to similar climatic causes.

Sparganiaceapollenites barungensis-pollen type. This is less indicative of former connections with other continents or of specific climates. The occurrence of this Australian Tertiary pollen type indicates former connections of Africa with South America and Australia. It also fits into the general pattern of an austral Gondwana connection indicated by *Microcachrys*, Winteraceae, and *Casuarina*. Dispersal routes may have been via South America—Antarctica to Australia or via the islands of the Indian Ocean. The possibility of bird dispersal must be taken into account here. The relatively young Tertiary age of this pollen type suggests either wider dispersal capabilities for the parent plant or an earlier unrecognized occurrence of the ancestral complex. The fossil record of Typhales, however, goes back only to the Palaeocene (cf. Muller, 1981). The extinction of the parent taxon of this pollen type at the end of the Tertiary in South Africa, Australia, and New Zealand is difficult to explain.

CONCLUDING REMARKS

The evidence discussed here not only throws light upon the relationship between Africa and Madagascar floras, but also on the contacts between Madagascar and South America as discussed by Raven and Axelrod (1974: 612). The data presented support the hypothesis that a common South American—Antarctic—African—Madagascar flora, which existed in the Cretaceous, became fragmented due to plate movements and that taxa common to Madagascar and South America today had their origin in the West Gondwana—Antarctic section of Gondwanaland. The evidence does not support the postulation of long-distance dispersal of some of these ancient taxa from Australia to Madagascar.

Long distance dispersal around the Indian Ocean before the Pliocene desertification in the Middle East, however, may have been responsible for the distribution of such taxa as *Adansonia*, *Hibbertia*, and *Nepenthes*.

The final problem on which the evidence discussed has considerable bearing is that of the impoverishment of the African flora in the course of the Tertiary. This phenomenon has been discussed by many authors, notably Moore (1973) for the palms and by Raven and Axelrod (1974). It would appear now that the hypothesis of local extinction, to explain the absence in Africa of many angiosperm taxa that are still present in South America, Madagascar, and SE Asia, finds support in the fossil record. A good example is the disappearance of the *Nypa* palm from tropical Africa at the end of the Eocene (Germeraad et al., 1968). For Cupanieae the disappearance from the microfossil record of the taxa characterized by the *Cupaniopsis* pollen type in the Palaeogene is documented by Jan du Chêne et al. (1978) and Salard-Cheboldaeff (1979). Their survival in South Africa well into the Miocene was presumably due to more stable and humid climatic conditions. *Ascarina* had become extinct over large areas much earlier (Muller, 1981).

It is thus evident that extinction may not have been a single event. It must have varied locally according to the severity of environmental changes associated with the maximum glaciation of Antarctica at the end of the Tertiary. Macchia must have spread during the Pliocene and Pleistocene when there were fluctuations of warm and cold water offshore (Axelrod & Raven, 1978; Tankard & Rogers, 1978). Some of these elements were already present in the summer rainfall climate of the Miocene and earlier and became adapted to summer droughts during periods of cold water currents. Axelrod and Raven (1978) considered the present mediterranean climate, in which the hardiest macchia taxa have survived and profoundly speciated, to have originated in the Late Pleistocene. The older periods (not earlier than 5 million years ago) of this type of climate were less intense (D. I. Axelrod, pers. comm.). On the basis of paleontological data, however, Hendey (1981b) postulated that the transition to the mediterranean type of climate could have occurred in the early Pliocene (5 million years ago). By that time the last relict occurrences of some warm temperate to subtropical taxa discussed here could have disappeared from the southwestern Cape (Coetzee & Rogers, 1982).

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